GEOLOGIC CONTROL OF VEGETATION IN THE PURISIMA HILLS, CALIFORNIA

KENNETH COLE
Department of Geosciences, University of Arizona, Tucson 85721

ABSTRACT

Five plant communities are recognized from the western Purisima Hills, Santa Barbara Co., California: closed-cone pine forest, douglas-fir forest, oak grassland, chaparral, and coastal sage scrub. The distribution of each community with respect to substrate type, fire history, and exposure was examined by mapping a 9.3 km^2 area. Bedrock geology and exposure were the principal factors affecting the distribution of the closed-cone pine forest and douglas-fir forest. Both communities were found primarily on north slopes of diatomaceous shale. To a lesser extent the other communities were most common on particular aspects and substrates: oak grassland grew mainly on gentle slopes, chaparral was predominant on south slopes of sandstone, and coastal sage scrub occurred on argillaceous substrates. The one recorded fire within the area had no recognizable affect on the sharp ecotones between communities.

The Purisima Hills of western Santa Barbara County, California, support a rich assemblage of vegetation types. Five distinct plant communities form mosaic patterns across rolling hills (Fig. 1). Coastal sage scrub, chaparral, oak grassland, closed-cone pine forest, and douglas-fir forest occur as discrete communities, usually with sharp ecotonal boundaries.

While the mosaic patterns of vegetational units in coastal California are readily apparent, the reasons for these patterns have been the subject of much discussion. They have been explained as successional (Cooper, 1922); a polyclimax controlled by different substrates (Shreve, 1972); the result of fire (Wells, 1962); and the result of differential moisture availability (Harrison et al., 1922). The sharp ecotones between some communities have been described as the result of volatile growth inhibitors produced by some aromatic shrubs (Muller et al., 1964) and herbivore impact between the communities (Bartholomew, 1970; Halligan, 1976). Some ecotones have been shown to be constant for at least 40 years (Bradbury, 1978).

Bishop pine (*Pinus muricata*), the dominant species of the closed-cone pine forest, forms a homogeneous cover with abrupt boundaries. Its distribution has been shown to be strongly influenced by edaphic factors (Lemmon, 1900; Westman, 1975), but stands have been reported on a variety of substrates (Wells, 1962; Griffin, 1964).

The variety of plant communities and substrate types present within a small area makes the Purisima Hills an ideal location for investigating relationships between substrate and community patterning. The sedimentary rock units are relatively undeformed allowing for a

MADROÑO, Vol. 27, No. 2, p. 79–89, 16 April 1980

FIG. 1. Vegetation patterns in the Purisima Hills. In the left foreground, chaparral grows on diatomaceous shale. Coastal sage scrub grows on mudstone in the right foreground. In the middleground, bishop-pine forest grows on diatomaceous shale on the left with coastal sage scrub and grassland on mudstone to the right. In the background, oak grassland grows on a sandstone terrace deposit.

clear understanding of stratigraphic relationships. This permits better understanding of soil origins because parent rocks are often obscured by thick soils and subtle lithologic differences could go unnoticed in the field.

The study area consists of rolling hills 190 to 400 m in elevation, 15 km east of the Pacific Ocean. The climate is greatly influenced by proximity to the ocean and frequency of summer fogs that offset the small amount of summer precipitation (Azevedo and Morgan, 1974). Rainfall is concentrated during the winter months (97 percent of recorded annual precipitation), while fog is concentrated in the summer (73 percent of foggy days/year: Cole, 1974). Precipitation has varied from a minimum of 8.5 cm in 1947 to a maximum of 97 cm in 1941 at the nearest long-term weather station (Santa Maria). The average annual precipitation 5 km south of the ridge is 33 cm. Temperatures do not fluctuate widely from day to night or seasonally.

METHODS

In this study, I compared vegetational, geologic, and topographic features by plotting them on a 1:8000 base map of the 9.3 km^2 study area. The vegetation and geology were mapped through observation and stereo aerial photography (U.S.G.S.). Five plant communities

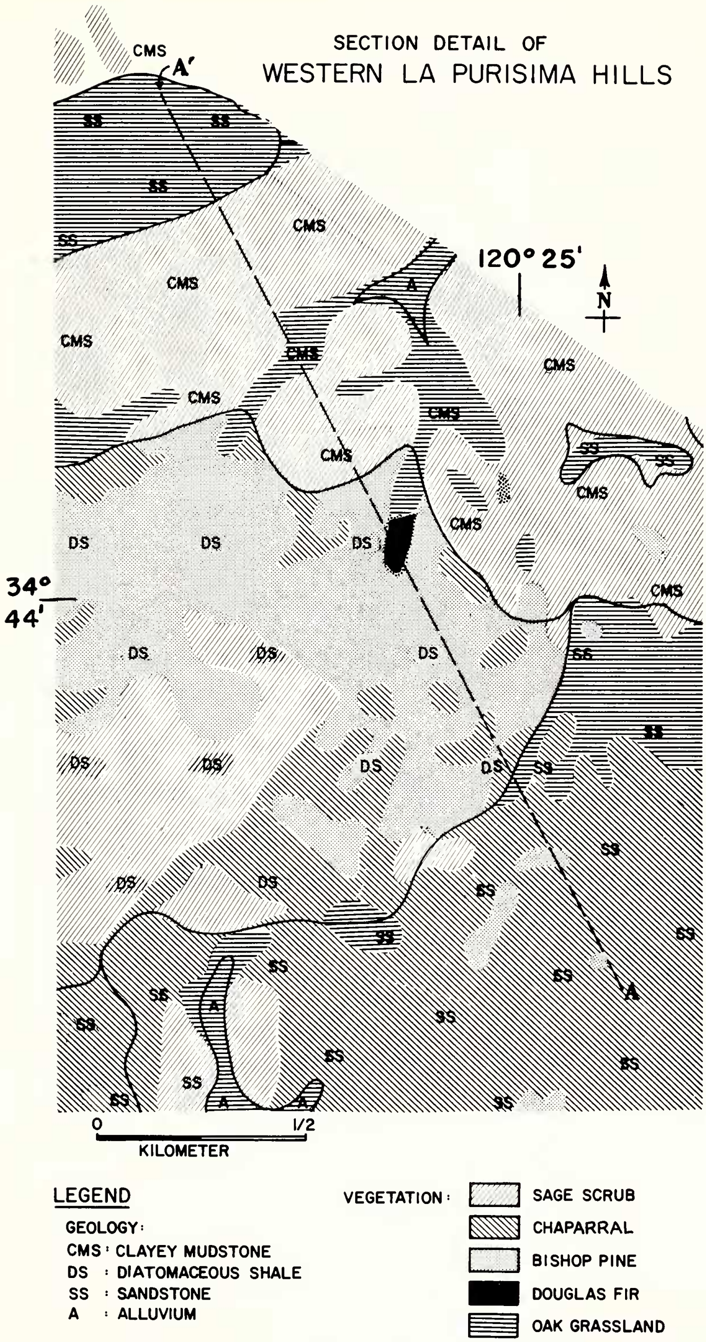

FIG. 2. Detail (about 25 percent) of vegetation-geologic map of the Purisima Hills.

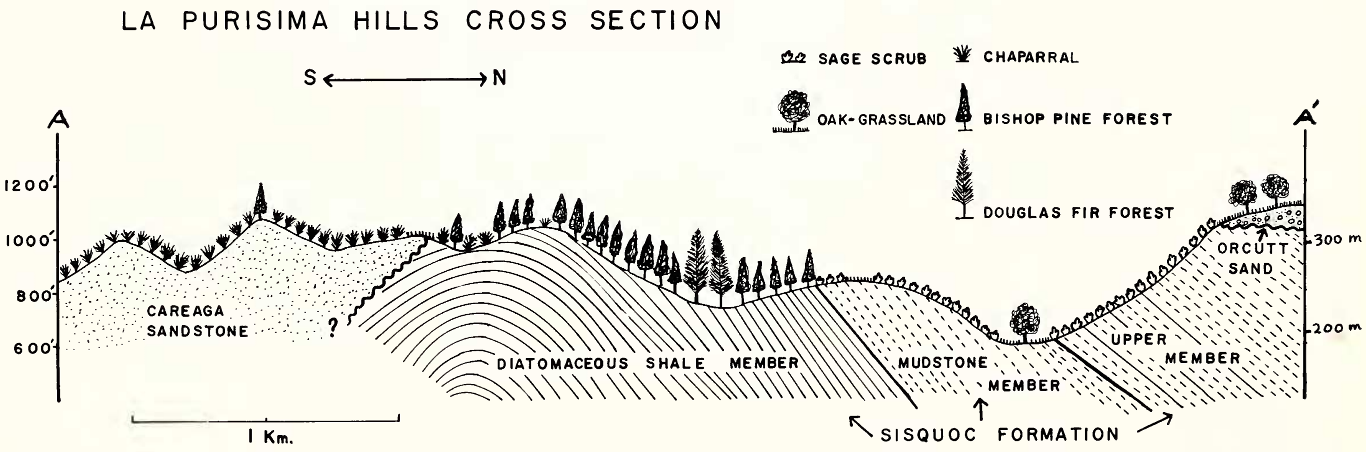

FIG. 3. Cross-section through line A-A′ of Fig. 2.

were recognized and mapped. Forty-one 30-m line intercepts provided quantitative data on the coverage of common plants in each vegetational unit. Taxonomic nomenclature follows Munz (1959).

Two composite soil samples from each substrate were made by combining 5 subsamples of surface soil from along a 30-m line intercept. Soil samples were tested using La Motte Soil Test Kit Model ST-1013. Eight distinct substrate units were mapped using the geologic nomenclature of Woodring and Bramlett (1950). The orientation of bedding planes was measured using a Brunton compass. The area occupied by each community type on each substrate was measured with a compensating polar planimeter from the map. These data were then split into north-facing slopes (270° to 90°) and south-facing slopes (90° to 270°).

Oven-dried rock samples from different substrates were tested for their water-retaining capacity by soaking in water for 30 minutes. The rocks were weighed several times as they dried to measure the remaining water. Rock volumes were measured by placing the rocks in plastic bags, submersing them in a filled container, and measuring the overflow.

RESULTS

Figure 2 is a portion of the map produced in this study. This portion was selected because it includes all five plant communities and an assortment of substrates. A cross-section through this area is illustrated in Fig. 3. The distribution of communities is discussed below.

Closed-cone pine forest. A dense forest dominated by bishop pine (*Pinus muricata* including some *P. remorata*) occurred on diatomaceous shale and sandstone. Only those areas where the coverage of these pines exceeded 50 percent were mapped as forest, even though isolated trees were spread over the entire area. The codominants in this forest were (in order of decreasing cover): *Quercus agrifolia, Heteromeles arbutifolia, Arctostaphylos crustacea, Vaccinium ovatum,* and *Rhus diversiloba.*

The majority (97 percent) of the area mapped as pine forest had diatomaceous shale substrates. Eighty percent of the mapped pine forest was located on north-facing slopes. Patches of forest were located on exposed sandstone hilltops accounting for 2.0 percent of the total forest cover. Not all diatomaceous shale substrates were covered by bishop pine. Good examples of both chaparral and sage scrub communities were found nearby on this substrate. The relative coverage of each community on each substrate is shown in Table 1. Bishop-pine forest covers a much larger percentage of the diatomaceous shale unit than any other substrate.

Douglas-fir forest. A small patch of douglas-fir forest (*Pseudotsuga*

TABLE 1. RELATIVE COVERAGE OF FIVE PURISIMA HILLS COMMUNITIES ON THREE SUBSTRATES. Percent coverage = area of community in substrate and slope class/total area in substrate and slope class. Community areas in hectares from which percent coverage values were calculated are given in parentheses. N = north-facing slope; S = south-facing slope.

	Diatomaceous shale		Sandstone		Mudstone	
Community	N	S	N	S	N	S
Bishop-pine forest	72% (99)	19% (24)	2.5% (1.7)	0.27% (0.90)	0.68% (0.83)	0.24% (0.22)
Douglas-fir forest	0.51% (0.70)	—	—	—	—	—
Oak grassland	1.7% (2.3)	—	40% (28)	14% (47)	15% (19)	5.7% (5.2)
Chaparral	11% (15)	43% (55)	40% (28)	71% (242)	4.1% (5)	—
Sage scrub	15% (21)	38% (48)	17% (12)	15% (49)	80% (98)	94% (85)

menziesii) was located in a shaded canyon on diatomaceous shale. The douglas-fir had a coverage exceeding 50 percent and was associated with *Vaccinium ovatum* and *Polystichum munitum.*

Oak grassland. The oak grassland community was dominated by introduced grass species with *Bromus rigidus, B. mollis,* and *Avena barbata* covering more than 70 percent of the ground. *Quercus agrifolia* reached its greatest concentrations (greater than 20 percent cover) in this community, although scattered oaks were present in every community. Seventy-four percent of the oak grassland was located on sandstone. This community is extensive in areas of low slope angle, and is probably underrepresented in this study because the flat areas adjoining the hills were mostly under cultivation.

Chaparral. The chaparral unit was defined as those areas dominated by chamise (*Adenostoma fasciculatum*) or manzanita (*Arctostaphylos* spp.). Chamise cover ranged from 30 percent on sandstone to greater than 80 percent on south slopes of diatomaceous shale. *Arctostaphylos pechoensis* var. *viridissima* was located predominantly on south slopes of sandstone, while *Arctostaphylos crustacea* dominated north slopes of diatomaceous shale. Chaparral was most common on southerly aspects and sandstone. Sandstone underlay 73 percent of the chaparral.

Coastal sage scrub. Areas of subligneous scrub vegetation were dominated by *Artemisia californica,* which usually had greater than

TABLE 2. CHARACTERISTICS OF FOUR SOILS FROM THE PURISIMA HILLS. Numbers are averages of 2 samples from each substrate.

	Diatomaceous shale	Porcelaneous shale	Clayey mudstone	Sandstone
pH	4.7	4.9	6.9	5.8
Nitrate (NO_4) (kg/ha)	29	21	18	9
Available potassium (kg/ha)	348	280	258	196
Replaceable calcium (ppm)	100	1250	2100	775
Chloride (ppm)	37.5	37.5	275	75
Sulfate (ppm)	50	50	75	50

40 percent cover. Other prominent species in this community were *Salvia mellifera, Brassica hirta, Lotus scoparius, Elymus condensatus,* and *Antirrhinum multiflorum.*

The coastal sage scrub community was most predominant on south slopes of clayey mudstone, covering 94 percent of these slopes. The community had a stunted appearance and lower total cover where it occurred on diatomaceous shale.

Soil tests (Table 2) suggest that soil pH is a factor in edaphic control on diatomaceous shale. Four samples taken in the closed-cone pine community, the chaparral community, and the coastal sage scrub community, all on diatomaceous shale, had pH values ranging from 4.6 to 5.0. The diatomaceous soils had relatively high nitrate and potash values and low calcium values.

In some cases geologic controls on plant distribution were apparent but no substrate or soil differences could be found. For example, bedding planes along the Purisima Anticline (Fig. 4) demonstrate that a chaparral community and a sage-scrub community are distinctly separated along a stratigraphic horizon. The pattern would appear fortuitous, or due to an aquifer, except for the fact that it continues through several hills and valleys as far as these rock strata are exposed. Both communities are growing on the same rock type, porcelaneous shale, a siliceous rock similar to the diatomaceous shale. The two soil samples taken from this substrate (one from each community) do not differ greatly. Comparison of 1954 and 1967 photos show that the boundary is stable and was not affected by a 1959 fire that burned both communities. No conclusion seems possible except that these communities are controlled by some unmeasured edaphic factor.

Substrate types differed in their ability to absorb and retain moisture. After one hour of drying, six samples of diatomite averaged 0.6 g H_2O/cm^3, or 60 percent retention. This compares with 32 percent for mudstone, 10–28 percent for sandstones, and 7 percent for granite.

FIG. 4. Sharp contact between chaparral (middle) and coastal sage scrub. This contact follows a stratigraphic horizon within the porcelaneous shale unit along the Purisima Anticline through several hills and valleys.

The diatomite samples still retained 30 percent water by volume after 135 hours. This compares favorably with previous reports on diatomite (Oakshott, 1957).

Discussion

Diatomaceous shale as a unique substrate type. The diatomaceous shale within the upper portion of the Sisquoc Formation ranks high on a world scale for thickness and purity. The Johns Manville Quarry, the largest diatomite quarry in the world, excavates the Sisquoc Formation 32 km south of the study area, in what used to be an extensive bishop-pine forest (Wieslander and Jensen, 1945). This substrate is composed almost entirely of the siliceous tests of diatoms with very few clay particles. Thus, the purity of the substrate determines both its unique biological nature and its economic value. Shallow, acidic soils are formed on diatomaceous substrates regardless of the plant community type. The substrate has a spongelike ability to absorb and retain water, but the availability of this water for plants remains an interesting area for further research.

Most outcrops of high quality diatomite support unique vegetation. In the Purisima Hills, bishop-pine forest and douglas-fir forest grow almost exclusively on diatomaceous substrates. Chaparral and coastal sage-scrub communities have lower species richness on diatomite than on adjacent substrates.

The diatomaceous substrates in the Purisima Hills support a large percentage of plants near the southern limits of their ranges (Cole, 1974). The population of douglas fir is disjunct 150 km south from its next occurrence along the coast (Griffin, 1964). Similarly, *Polystichum munitum, Vaccinum ovatum, Arbutus menziesii,* and *Lupinus arboreus* were found only on diatomaceous substrates in the area. The diatomaceous shale substrate in the Purisima Hills supports a large percentage of plants also located on the northern Channel Islands (21 out of 62 plants collected on this substrate). It is noteworthy that much of Santa Cruz Island is underlain by diatomaceous shale.

Edaphic control of the distribution of bishop pine. The distribution of *Pinus muricata* is strongly influenced by substrate type. Although stands of forest are located on all substrates, the densest and most extensive forests are on diatomaceous shale. The sandstone substrate supporting pine forest is similar to the diatomaceous shale substrate in that the forests are located in pockets of quartz-rich sand with little clay content.

Other localities in Santa Barbara County conform well to the model of edaphic control in the Purisima Hills. At the Johns Manville Quarry and Pine Canyon at Graciosa Ridge, extensive forests grow (or grew) on diatomite of the Sisquoc Formation. The bishop pines on nearby Vandenburg Air Force Base are less restricted to the diatomite units with the most extensive groves located on adjacent sandstones (Paul Zedler, pers. comm., 1979).

Pinus muricata is distributed discontinuously along 1400 km of Pacific coastline from near Oregon to Baja California. It occurs on a variety of soils, but most are shallow, acidic, and poorly drained (Vogl et al., 1977).

Substrate restriction in the study area is probably the result of reduced competition from the surrounding chaparral and sage communities, rather than an inability of the pine forest to survive on other substrates. The situation is similar to that of other moisture-loving species that are restricted to acidic substrates in xeric habitats (Kruckeberg, 1969).

Edaphic control of other communities. Wells (1962) also concluded that chaparral communities dominate on siliceous substrates while coastal sage-scrub communities dominate on argillaceous substrates. This has been explained as a result of moisture availability (Harrison et al., 1971). Oak grassland is best developed on gentle north slopes with deep soils.

Fire roads plowed during the last 20 years were invaded by coastal scrub communities even in dense chaparral thickets. This may support Cooper's (1922) suggestion that coastal sage scrub is successional to chaparral. However, an extensive fire in 1959 did not affect the ecotonal placement between the communities. The only recognizable change occurring in the area since the first stereo aerial photographs were taken in 1954 was a thinning of the closed-cone pine forest in the fire area. Although this fire had no affect on community patterning, a more (or less) severe fire might.

Edaphic restrictions of these more widespread communities are not as definite as those of the closed-cone pine forest. Perhaps the best explanation for the patterning between these communities lies in the past; events have occurred that allowed one community to expand at the expense of another, while each community has maintained a core where it is most favorably adapted to substrate and microclimate. The present distributions could be described as: (1) stable, changing only with long-term climatic or other changes; (2) stable, dominant plants controlled by some edaphic or climatic factors yet unmeasured; or (3) changing so slowly that 24 years of aerial photography could not demonstrate a change.

Geologic control of vegetational patterns. Vegetational boundaries on steep slopes in temperate habitats often correlate strongly with underlying geology. Deep soil development is prevented by steep topography and climatic limits on vegetation are less controlling than in more severe habitats. As a result, plants compete for dominance on a variety of substrates. Although each community could probably occupy any substrate successfully, only the most competitive community will dominate any given substrate.

The importance of these relationships has been obscured in the past by comparison of substrates and vegetation over large areas. There is no reason to expect a community restricted to a particular substrate to exhibit this restriction 50 km away because many climatic factors may have changed over that distance. Another problem is the variable nature of rocks themselves. A formation of sandstone may include layers of shale or limestone not indicated on a large-scale geologic map. Stratigraphic knowledge and the ability to do simple, projective geological mapping will often uncover plant-rock relationships that would otherwise escape notice. One last complication is that two very different substrates can yield similar soils and vegetation. For example, diatomite and siliceous sandstone both can produce shallow acidic soils capable of deep water percolation.

The vegetational mosaics of coastal California provide unique opportunities for the study of the interrelationships between substrate and vegetation. Unfortunately, many plant ecologists have turned away from this kind of study because the variability inherent in rocks is probably as great as the variability within the vegetation itself. Nevertheless, there is great potential in the study of these correlations.

Acknowledgments

I thank Richard Vogl who inspired me to begin this study. I also thank James Henrickson, Martin Stout, Dale Boregard, Paul Martin, Willard Van Asdall, James Griffin, Geoffrey Spaulding, Paul Zedler, Deborah Gaines, and Melinda Cole for their assistance and comments. I am grateful to the Union Oil Company for permission to work on their land. This work was supported in part by a grant from the Associated Students Graduate Research Commission at California State University, Los Angeles and by NSF Grant DEB 75-13944-A01 to Paul S. Martin.

Literature Cited

Azevedo, J. and D. L. Morgan. 1974. Fog precipitation in coastal California forests. Ecology 55:1135–1141.

Bartholomew, B. 1970. Bare zones between California scrub and grassland communities. Science 170:1210–1212.

Bradbury, D. 1978. The evolution and persistence of a local sage/chamise community pattern in southern California. *In*: Association of Pacific Coast Geographers Yearbook, vol. 40, Oregon State Univ. Press, Corvallis.

Cole, K. L. 1974. Edaphic restrictions in the La Purisima Hills with special reference to *Pinus muricata* M.S. thesis, California State Univ., Los Angeles.

Cooper, W. C. 1922. The broad sclerophyll vegetation of California: an ecological study of the chaparral and its related communities. Publ. Carnegie Inst. Wash. 319.

Halligan, J. 1976. Relationship between animal activity and bare areas associated with California sagebrush in annual grassland. J. Range. Management 27:358–362.

Harrison, A., E. Small, and H. Mooney. 1971. Drought relationships and distribution of two Mediterranean-climate California plant communities. Ecology 52:869–875.

Kruckeberg, A. R. 1969. Soil diversity and the distribution of plants with examples from western North America. Madroño 20:129–154.

Lemmon, J. C. 1900. Handbook of West American cone bearers. Oakland Press, Oakland, California.

Oakshott, G. B. 1957. Diatomite. California Div. Mines Bull. 176:183–193.

Muller, C. H., W. H. Muller, and B. L. Haines. 1964. Volatile growth inhibitors produced by aromatic shrubs. Science 143:471–473.

Munz, P. A. 1979. A California flora. Univ. California Press, Berkeley.

Shreve, F. 1927. The vegetation of a coastal mountain range. Ecology 8:27.

Vogl, R. J., W. P. Armstrong, K. L. White, and K. L. Cole. 1977. The closed-cone pines and cypresses. *In*: Terrestrial vegetation of California, M. G. Barbour and J. Major, eds., pp. 295–358. Wiley-Interscience, New York.

Wells, P. V. 1962. Vegetation in relation to geologic substratum and fire in the San Luis Obispo Quadrangle, California. Ecol. Monogr. 32:79–103.

Westman, W. E. 1975. Edaphic climax pattern of the pygmy forest region of California. Ecol. Monogr. 45:109–135.

Weislander, A. E. and H. A. Jensen. 1945. Vegetation types of California. (Blueprint of statewide vegetation-type map.) U.S.D.A. For. and Range Exp. Sta., Berkeley.

Woodring, W. P. and N. M. Bramlette. 1950. Geology and paleontology of the Santa Maria district, California. U.S.G.S. Prof. Pap. 222.

(Received 21 Dec 1978; revision received 11 Dec 1979; accepted 31 Dec 1979.)